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MORPHOLOGICAL RESPONSES OF WHEAT (*Triticum aestivum*, L.)
TO CHANGES IN PHYTOCHROME PHOTOEQUILIBRIA,
BLUE LIGHT, AND PHOTOPERIOD

by

Charles Barnes

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Plant Science
(Plant Physiology)

Approved:

UTAH STATE UNIVERSITY
Logan, Utah

1990

In memory of

Joseph Delmer Hoyt, 1947-1980

John Benton Barnes, 1947-1985

friends and brothers

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Charles Barnes

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LIST OF SYMBOLS AND ABBREVIATIONS

ζ (zeta)	Red:Far-red Radiation Ratio
ϕ (phi)	P_{fr}/P_{total}
FR	Far-red radiation (700-800 nm)
P_{fr}	Phytochrome, far-red form
P_r	Phytochrome, red form
P_{total}	Total Phytochrome
$I(\lambda)$	Photon Fluence Rate (at λ nm)
HPS	High-pressure Sodium
LAI	Leaf Area Index
LED	Light Emitting Diode
MH	Metal Halide
PAR	Photosynthetically Active Radiation
PPF	Photosynthetic Photon Flux
R	Red light (650-700 nm)
SED	Spectral Energy Distribution

ABSTRACT

Morphological Responses of Wheat (*Triticum aestivum* L.) to Changes
in Phytochrome Photoequilibria, Blue Light and Photoperiod

by

Charles Barnes, Doctor of Philosophy

Utah State University, 1990

Major Professor: Dr. Bruce Bugbee
Department: Plants, Soils and Biometeorology

Wheat (*Triticum aestivum*, L.) plants were exposed to three different levels of phytochrome photoequilibria (ϕ), two different photoperiods, end-of-day far-red radiation, two different levels of blue (400-500 nm) light, three levels of photosynthetic photon flux (PPF), and two types of high intensity discharge lamp types. Tillering was reduced by lowered ϕ , by reduced amounts on blue light, and by end-of-day far-red. Main culm development was increased by lowered ϕ , by increased PPF, and was reduced by shortened photoperiod and by reduced blue light. Leaf length was increased by increased PPF, lowered ϕ , and reduced blue light but was not affected by photoperiod, end-of-day far-red or lamp type. Dry-mass accumulation increased under increasing PPF but was unaffected by other treatment in these experiments.

(69 pages)

INTRODUCTION

Tillering in wheat (Triticum aestivum L.) is a morphological response to favorable environmental conditions. It is an effective and important strategy for wheat plants grown in the field, where plant response must vary with resource availability and environmental conditions. Under the constant conditions maintained in controlled environments, however, such as those used in NASA's Controlled Environment Life Support System (CELSS) project, a variable plant response is neither necessary nor desirable. One goal of wheat production in a CELSS is to maximize seed yield per unit time. The generation of a community of low-tillering wheat plants might help accomplish this goal by increasing crop uniformity. A more uniform crop, composed mainly of primary heads, should mature several days earlier than crops with multiple, late-maturing tillers, which are about 10% less productive than primary culms. More uniform crops may, therefore, have both a shorter life cycle and an increased harvest index, thus helping maximize seed yield per unit time.

Wheat breeding has developed "uniculm" (single head) breeding lines that produce plants with a single shoot in the field. These same cultivars produce multiple tillers when grown in low-stress environments. Thus, genetic approaches alone do not appear to be adequate in creating low-tillering wheat crops.

Cultural and environmental methods of reducing tillering must also be considered. Manipulation of radiation quantity (intensity, duration) and quality (spectral energy distribution) is a promising approach to solving this problem.

The primary objective of this research was to determine if manipulation of radiation quantity and quality can be effective in significantly reducing the amount of tillering in wheat plants. Additional goals were to test the effects of spectral manipulation on other plant responses such as dry-mass accumulation, leaf elongation, and the rate of development of the main shoot.

MORPHOLOGICAL RESPONSES OF WHEAT TO CHANGES IN PHYTOCHROME PHOTOEQUILIBRIA

Abstract

Wheat plants (*Triticum aestivum* L., cultivars Fielder, Veery 10 and Yecora Rojo) were grown at the same photosynthetic photon flux (PPF), $200 \mu\text{mol m}^{-2} \text{s}^{-1}$, but with phytochrome photoequilibria ($\phi = P_{fr}/P_{total}$) values of .81, .55 and .33. Tillering decreased 43% and 56% in plants grown at ϕ values of .55 and .33, compared to plants grown at $\phi = .81$. Main culm development (Haun stage) increased slightly with decreasing ϕ and the length of leaf sheaths, but not lamina, also increased with decreasing ϕ . Dry-mass accumulation was not affected by different levels of ϕ . Three levels of irradiation (100, 200 and $400 \mu\text{mol m}^{-2} \text{s}^{-1}$) and two lamp types, metal halide and high-pressure sodium, were also tested. Increasing PPF increased dry-mass, tillering, and Haun stage. There was no difference in plant growth or development under metal halide versus high-pressure sodium lamps, except for total leaf length, which was increased by high-pressure sodium lamps (49.5 versus 44.9 cm, $P < .01$).

Introduction

Wheat plants (*Triticum aestivum* L.) grown in optimized, controlled environments produce more shoots (tillers) with seed-bearing heads than field-grown plants.

This is a response to high levels of nitrogen, ample water, elevated CO₂, and high irradiation from artificial sources--conditions typical of those used in crop production studies for NASA's Controlled Environment Life Support System (CELSS) project. Tillers produced in response to these conditions mature later than the primary shoot (main culm) and have a harvest index (percent edible biomass) that is about 10% lower than the primary shoot, thus lengthening crop life cycle and reducing yield per day (4). Artificial radiation sources typically create spectral energy distributions (SED) different from sunlight SED and elicit plant responses different from those caused by sunlight. We sought to reduce tillering of wheat, by manipulating the SED of the radiation source, in a controlled environment. Such a reduction may help increase yield per day by allowing earlier harvest and by increasing the harvest index of the crop.

Effects of radiation. Plant growth and development are strongly influenced by radiation quantity (intensity), its duration (photoperiod), and its quality (SED). At non-saturating levels, the effect of radiation quantity is a simple growth response, for example, higher intensities result in larger plants via higher CO₂ assimilation. Radiation quality and duration control the activity of plant photoreceptors (phytochrome and the blue-UV light receptors), that ultimately results in various morphological responses, such as tillering and stem elongation.

The objective of this study was to determine whether morphological responses such as tillering in wheat could be manipulated by changing the SED of radiation sources. In my experiments, I tested three levels of predicted P_{fr}/P_{total} (ϕ)¹, $\phi = .81, .55$ and $.33$; two types of high-intensity discharge lamps, high-pressure sodium and metal halide; and three radiation intensities, 100, 200, and 400 $\mu\text{mol m}^{-2} \text{s}^{-1}$.

Response to radiation quantity. Evans *et al.* (12) tested the tillering response of five wheat cultivars to radiation quantity over a range of normal sunlight irradiances. Increasing levels of radiation resulted in a linear increase in the amount of tillering in all cultivars tested. Friend *et al.* (13) also found that plant dry-mass and rate of development increased with increasing radiation intensity.

Response to radiation quality. Tillering in grasses is affected not only by radiation quantity but also by its quality (SED), which controls the activity of at least two plant photoreceptors, the blue light receptor(s) and phytochrome. The characteristic SED of artificial radiation sources used in controlled environments determines the activity of each photoreceptor. Responses to blue light appear to be controlled by the absolute amount of blue light (400-500 nm) received by the plant. Phytochrome responses, on the other hand, are controlled by the ratio of the amount of phytochrome in the active form (P_{fr}) to total phytochrome (P_{total}), or P_{fr}/P_{total} (symbol ϕ). This ratio (ϕ) can be predicted from the SED of the

¹ Abbreviations: R, red light (650-700 nm); FR, far-red radiation (700-800 nm); P_{fr} , phytochrome in the far-red absorbing form; P_r , phytochrome in the red-absorbing form; P_{total} ($= P_r + P_{fr}$), the total amount of phytochrome; ϕ ($= P_{fr}/P_{total}$), ratio of the amount of phytochrome in the active form to total phytochrome; ζ , ratio of red to far-red irradiation, generally 660:730 nm

radiation source. An approximation of ϕ is the ratio of the relative amounts of radiation at the peak absorption wavelengths for each form of phytochrome, usually centered around 660 nm for P_r and 730 nm for P_{fr} , or 660:730 (symbol ζ).

Response to ζ Ratios. Most investigations of the effect of different ζ ratios (and therefore, different ϕ) on tillering have manipulated ζ by irradiating plants with artificial sources or adding supplemental R or FR radiation to create ζ ratios higher or lower than sunlight (ζ for sunlight is approximately 1.15). Casal *et al.* (5) exposed *Lolium multiflorum* (annual ryegrass) to red:far-red ratios ($\zeta = 650:725$ nm) of 1.62 and .84. The relative tillering rate in the lower ζ treatment ($\zeta = .84$) was reduced by half in vegetative plants and by a third in plants that reached the reproductive stage. The mean tiller number was reduced by 30%. In a later experiment, Casal *et al.* (8) found that reducing ζ from 1.44 to .62 again resulted in large reductions in tillering (from 24 to 14 tillers per plant), but as ζ was further reduced to .03, the number of tillers *increased* (from 14 to 19).

Deregibus *et al.* (11) altered the red:far-red ratio ($\zeta = 650:725$) by adding R with light emitting diodes at the base of *Paspalum dilitatum* Poir. and *Sporobolus indicus* [L.] R. Br. plants. They found that increasing the red:far-red ratio to twice that of sunlight (i.e. from 1.1 to 2.2) significantly increased tiller number in *P. dilitatum* (from 15 to 45), but not in *S. indicus*. Wheat plants produced an average of 7.5 and 7.1 tillers in response to ζ (645:735) ratios of 5.0 and 1.5, according to tests by Kasperbauer and Karlen (20).

Response to Planting Density. Planting density affects the phytochrome balance in plants because plants selectively reflect, transmit and absorb radiation, thus altering the SED within the plant canopy. In sparse canopies, plants affect other plants mainly by reflecting more FR than R radiation, causing neighboring plants to detect a decrease in ζ (and, therefore, in ϕ). Plants detecting this decrease in ζ respond by increasing internode elongation and thus may avoid being shaded by other plants (1, 2, 3, 19).

Plant leaves also act as radiation filters, transmitting about 40% of FR, while absorbing about 85% of all visible wavelengths, including R (19). This filtration is especially important in densely planted canopies, where radiation reaching the bottom of the canopy becomes rich in FR and low in R. The lowering of ζ (and, therefore, ϕ) by plant leaves is the result of selective absorption of radiation by plant pigments, mainly chlorophyll, which strongly absorb radiation of wavelengths 400-700 nm and transmit nearly all radiation with wavelengths beyond 700 nm.

Holmes and Smith (17) characterized the selective attenuation of daylight in a wheat canopy with changes in canopy depth and planting density. The value of ζ decreased from 1.15 (unfiltered sunlight) above the canopy to a minimum of .2 at a leaf area index of 3.5 - 4.0.

Natural and Simulated Shadelight. Lower ζ ratios in dense canopies due to natural filtration by leaves (shading) appear to have the same effect as lower ζ ratios artificially created in controlled environments. Lowering of ζ by either means results in the morphological responses of increased stem elongation (18, 24, 26) and reduced tillering (6, 20). Holmes and Smith (18) observed a significant increase in stem elongation in *Curcubita pepo* L. and *Chenopodium album* grown in the shade of a simulated wheat canopy. Casal *et al.* (6) found a positive correlation between lowered ζ and reduced tillering in densely planted communities of *Paspalum dilitatum* and *Lolium multiflorum*.

Relationship of ζ and ϕ . Smith and Holmes (17) characterized the relationship between ζ and ϕ for several natural and artificial radiation sources. They found that values for ϕ increased linearly from a minimum of .04 (under a dense canopy) to about .54 (typical sunlight ϕ) for corresponding ζ values of .05 and 1.15, respectively. For ζ values from approximately 1.15 to 16, ϕ values asymptotically approached a maximum of about .75.

Recent estimates indicate, however, that the maximum possible phytochrome balance and the value of ϕ for typical sunlight given by Smith and Holmes are too low. Under irradiation with monochromatic R, the maximum possible ϕ in vivo may be as high as .89 (22); this upward revision of maximum ϕ raises the ϕ for sunlight to about .73 (23).

Direct measurement of phytochrome in etiolated plants using a dual-beam spectrophotometer (14, 18) has shown that changes in the ζ ratio affect phytochrome photoequilibria (ϕ). Unfortunately, this method cannot be used on mature green tissue due to the interference of chlorophyll and other pigments, making it necessary to develop methods of predicting ϕ from measurements of SED.

Methods of Estimating Phytochrome Activity. The most common method of estimating ϕ has been to use measurements of ζ to predict ϕ , but the reliance on narrow wavebands centered around 660 and 730 nm is inaccurate under artificial sources, especially those with a strong blue component. We used a more accurate method of predicting ϕ developed by Gardner and Graceffo (14) and refined by Sager *et al.* (23). In this method, the intensity of radiation at each wavelength from 300-800 nm is measured with a spectroradiometer, and the relative amount of conversion of P_r to P_{fr} and P_{fr} to P_r at each wavelength is summed over the entire range of wavelengths to give P_{fr}/P_{total} .

Materials and Methods

Cultural Procedures. These experiments were conducted in a series of five trials. Each treatment contained 24 (Trial 1) or 20 (Trials 2-5) pots. Wheat (*Triticum aestivum* L., cvs Fielder, Veery 10 and Yecora Rojo) seeds were sown into soilless media (equal parts peat moss, perlite and vermiculite) in plastic pots (120 X 120 X 100 mm) and germinated at 23 °C in a multi-sectioned, controlled-environment growth chamber. All plants in trials 1-3 were cv. Fielder. In trials 4 and 5, ten plants were Veery 10 cultivar and 10 were Yecora Rojo.

All sections of the growth chamber were connected to a common air conditioning system, so CO₂ concentration, humidity, and temperature were nearly identical. Temperature was continuously monitored with a shielded, Type E, 24 gauge thermocouple in the center of each unit. Thermocouples were connected to a datalogger (Campbell Scientific model 21x). The average daily temperature was calculated and maintained at 21.5 + .5° C in all sections throughout each trial. The atmosphere was enriched with CO₂ to approximately 1000 $\mu\text{mol mol}^{-1}$ to maximize the rate of assimilation. Plants emerged uniformly in each treatment after three days and were thinned to one plant per pot five days after planting. All plants were then of approximately equal size. Pots were rotated every 3-4 days to ensure uniform exposure to treatments. The planting density in each section, approximately 40 plants m⁻², was believed to be sparse enough to minimize the effect of reflected FR radiation (1). Pots were watered daily with ca. 300 mL of a complete nutrient solution.

Spectral Treatments - Trials 1 and 2. Two phytochrome photoequilibrium (ϕ) treatments with nearly identical total PPF ($200 \mu\text{mol m}^{-2} \text{s}^{-1}$) were created. Plants in the control treatment were grown under white light ($\phi = .81$) from a 400-W metal halide (MH) lamp (Sylvania) passing through a 5 cm water bath and 9 mm Plexiglass barrier (Dupont Lucite acrylic). Plants in the reduced phytochrome photoequilibrium ($\phi = .55$) treatment were exposed to radiation from a 1000-W MH lamp (Sylvania) and two 500-W incandescent spotlights filtered as above and additionally filtered through a light blue (Rosco R64 "Light Steel Blue") filter (creating a $\phi = .55$). In addition, three levels of radiation intensity (PPF = 100, 200, and $400 \mu\text{mol m}^{-2} \text{s}^{-1}$) were created in three separate sections of the growth chamber with 1000-W high-pressure sodium (HPS) lamps filtered through 5 cm chilled water bath and 9 mm of Plexiglas and additionally filtered through layers of black neutral density (fiberglass) screen to uniformly reduce PPF to the appropriate level. All HPS treatments created $\phi = .85$.

Trials 3 - 5. Three phytochrome photoequilibrium treatments were tested. Two were the same as in Trial 1 above ($\phi = .81$, and $\phi = .55$); one additional reduced ϕ treatment was created by exposing plants to radiation from two 1000-W metal MH lamps (Sylvania) and three 500-W incandescent spotlights filtered through water and Plexiglas as described above and additionally filtered through a dark blue (Rosco R80 "Primary Blue") filter, creating a ϕ of .33 with a total PPF of $200 \mu\text{mol m}^{-2} \text{s}^{-1}$. HPS lamps and different radiation intensities were not tested in trials 3-5.

Radiation Measurements. Measurements of PPF and ϕ were made at the top of the plant canopy in each section. PPF was measured every 3-5 days throughout each trial. The height of plant trays was adjusted to maintain the appropriate PPF intensity at the canopy top. Phytochrome photoequilibria (ϕ) were determined with a computer-driven spectroradiometer (Hewlett Packard model HP-85 computer and an Optronics model 740 A spectroradiometer) using the method of Sager *et al.* (23). Photosynthetic photon flux (PPF) and the relative contribution of blue photons to total photosynthetically active radiation (PAR) in each treatment were determined from the same spectroradiometric data. PPF data were corroborated with a quantum sensor (Li-Cor model LI-188B). Plants grown in white light ($\phi = .81$) received $200 \mu\text{mol m}^{-2} \text{s}^{-1}$ of continuous PPF, of which $50 \mu\text{mol m}^{-2} \text{s}^{-1}$ were blue (400-500 nm) photons. Plants in the reduced phytochrome photoequilibrium ($\phi = .55$ and $.33$) treatments also received continuous PPF of $200 \mu\text{mol m}^{-2} \text{s}^{-1}$, of which approximately 67 and $117 \mu\text{mol m}^{-2} \text{s}^{-1}$ were blue photons, respectively. HPS lamp treatments (PPF = 100, 200, and $400 \mu\text{mol m}^{-2} \text{s}^{-1}$) received approximately 6, 12, and $25 \mu\text{mol m}^{-2} \text{s}^{-1}$ of blue photons, respectively, while creating a $\phi = .85$ in each treatment.

Plant Measurements. At each harvest, tiller number, main culm development (Haun stage), and shoot dry weight (g) were determined. Haun stage is a measure of the development of cereal plants based on a comparison of the length of the latest leaf to emerge to the length of the previous leaf (15, 21). Detailed harvest procedures were as follows: **Trial 1.** Eight plants were harvested from

each treatment section at 23, 25 and 28 days after emergence. **Trials 2 and 3.**

Harvests were 8, 6, and 6 plants taken 16, 20 and 24 days after emergence. **Trials 4 and 5.** Harvests of five plants each of Veery 10 and Yecora Rojo were made 16 and 24 days after emergence. The lengths of the leaf sheath and lamina for each of the first five leaves were measured at each harvest.

Results and Discussion

Effect of Radiation Intensity. Increased levels of PPF resulted in increased numbers of tillers produced (Fig. 1) and increased amounts of dry-mass accumulated (Fig. 2). Tillering data are similar to the results of Evans (12), who found that tiller number increased linearly with increasing solar radiation. Plants grown in the reduced phytochrome photoequilibrium (ϕ) treatments produced fewer tillers than would be predicted by radiation intensity alone (Fig. 1). To determine if this effect was due to reduced ϕ or to some other cause, we compared dry-mass accumulation for all treatments tested, and found dry-mass to be a linear function of PPF intensity (Fig. 2). Plants grown in the reduced ϕ treatment, therefore, did not accumulate more dry-mass in response to PPF than did plants grown in other treatments. The data in Figures 1 and 2 also indicate that dry-mass was positively correlated with tiller production; that is, larger plants produced more tillers (Fig. 3). This was true for all treatments in Trials 1-3, except for the reduced ϕ treatments, which produced fewer tillers than would be predicted on the basis of dry-mass accumulation (determined by ANOVA, $F = 9.76$, $P < .05$). These results suggest that the observed reductions in tillering cannot be attributed to differences in either radiation intensity or plant size and thus are assumed to be a photomorphogenic mediated by phytochrome.

Increasing radiation intensity also resulted in an increase in the development of the main culm (Haun Stage). Plants exposed to lower ϕ increased their rate of

main culm development more than would be predicted by PPF alone (Fig. 4).

Haun stage was reduced more rapidly at lower PPF levels (Fig. 4). This may be because development at low PPF is carbohydrate limited, thus development would stop at the light compensation point (about $50 \mu\text{mol m}^{-2} \text{s}^{-1}$).

Effect of reduced phytochrome photoequilibria. Changing ϕ from .81 to .33 reduced tiller number an average of 50% by the final harvest of each trial (Fig. 5A; $P = .0005$, $F = 49.1$, trials 4 and 5). The largest effect of ϕ on tiller production occurred between ϕ treatments of .81 and .55. There was a small additional reduction in tillering with a further reduction of ϕ to .33 (Trials 3-5; Fig. 5A-F). For cvs Yecora Rojo and Veery 10 combined in trials 4 and 5, the average reduction in tillering was 47% for $\phi = .81$ and .55 ($P < .01$, based on LSD - student's t) and 27% for $\phi = .55$ and .33 ($P < .1$, based on LSD, based on LSD - student's t).

Casal *et al.* (5, 8) studied the effect of phytochrome on tillering in *Lolium multiflorum*, but based their findings on spectral measurements of ζ rather than ϕ . Values for ϕ values can, however, be estimated from their ζ . Values of ζ of 1.62 and .84 (5) correspond to ϕ of .74 and .59 and ζ of 1.44 and .62 (8) correspond ϕ of .70 and .53. These ζ thus approximate to the ϕ values (.81 and .55) used in this study. The tillering reduction in wheat of 47% in our study is consistent with the 30% and 41% reductions in *L. multiflorum* found by Casal *et al.* (5, 8). The much higher planting densities (123 m^{-2} compared to 40 m^{-2} in our studies) used by Casal *et al.* (5) could act to reduce tillering, altering ζ by transmitting and reflecting more FR within the canopy. Also, Casal *et al.* (8) altered the ζ ratio by

irradiating only the plant base with incandescent lamps, whereas we altered the ϕ of the radiation source above the plants.

Our results for very low ϕ , however, are substantially different from those of Casal *et al.* (8), who found an *increase* in tillering with ζ reductions below .62 (similar to ϕ of about .53). Lower ϕ (which simulates deep shading) should result in an additional reduction in tillering. The increase in tillering with lower ζ (hence lower ϕ), found by Casal *et al.* (8), is difficult to interpret and this discrepancy is not addressed in their manuscript. The effect of reducing ϕ from .55 to .33 was less significant in our study (27% tillering reduction, $P < .1$) than the initial reduction from .81 to .55 (47% tillering reduction, $P < .01$), but the response is in the expected direction.

Of the three cultivars tested, cv Veery 10 tended to tiller less than cvs Yecora Rojo and Fielder in all treatments. Surprisingly, cv Fielder, which was selected for this study because of its high tillering rate, tillered about the same as cv Yecora Rojo, a typically low tillering cultivar (Fig. 5).

Effect of Reduced Phytochrome Photoequilibria on Leaf Extension. Leaf sheath and lamina length were measured for cvs Veery 10 and Yecora Rojo in Trials 4 and 5. The reduction in ϕ did not affect leaf lamina length in either cultivar tested in either trial (data not shown). The sheath length of early developing leaves increased slightly (about half of all leaves 1-3 tested increased - half showed no trend) with decreasing ϕ . Later developing leaves more clearly showed this trend, especially between ϕ treatments of .81 and .55 (Fig. 6A-D). These results

are consistent with the results of Casal *et al.* (7), who found that while lowered ζ ratios increased sheath length of leaves in three species of grass - *Lolium multiflorum*, *Sporobolus indicus*, and *Paspalum dilitatum* - only one of these species, *Lolium multiflorum*, increased lamina length in response to lower ζ .

Effect of Reduced Phytochrome Photoequilibria on Haun Stage. A relationship between phytochrome and development rate has not been previously reported in grasses. In all three cultivars tested, reductions in ϕ resulted in a small, but consistent increase in the rate of development (measured as Haun stage) over the range of ϕ values tested ($F = 56.5$, $P = .0004$, for trials 4 and 5). As with tillering, the main effect occurred between ϕ treatments of .81 and .55 ($P < .05$, based on LSD - student's t), with a less pronounced effect between $\phi = .55$ and .33 ($P < .1$, based on LSD - student's t). In trials 4 and 5, the increase in Haun stage in response to lower ϕ was noticeable at day 16 (Fig. 7B-C). In trial 3, the effect was observable at day 20 (Fig. 7A). Plants that increased in Haun stage in response to low ϕ treatments produced fewer tillers but just as much dry-mass. These data, and those in Figures 4 and 7 suggest that plants exposed to lower ϕ may be diverting resources away from tillering to more rapid development of the main culm.

Effect of Lamp Type on Wheat Morphological Responses. No difference was found in tiller number, Haun stage, or dry-mass for wheat cv Fielder grown under HPS vs MH lamps at the same PPF ($200 \mu\text{mol m}^{-2} \text{s}^{-1}$) in trials 1 and 2. Leaves of

plants grown under HPS lamps were, however, significantly longer ($P < .01$ - LSD, based on students's t) than those grown under MH lamps (49.5 vs 44.9 cm).

Effect of Blue Light on Wheat Morphological Responses. The possible complicating effects blue light in the treatments being created in this study need to be addressed. Wheat responds to increasing amounts of blue light by producing more tillers, provided the phytochrome balance (ϕ) is held constant. In previous work, for example, we found that increasing the amount of blue light from 2 to 50 $\mu\text{mol m}^{-2} \text{s}^{-1}$ increased tillering by 42% in wheat for two treatments where ϕ was approximately equal ($\phi = .81$ and $.84$). However, when ϕ is reduced and the amount of blue light is increased, as in the two reduced ϕ treatments in this study, these become competing or conflicting forces. The increasing blue light promotes more tillering in wheat while the reduced ϕ acts to inhibit the same response. Wheat appears to be more responsive to reductions in ϕ than to the increased levels of blue light. Specifically, in the present study, there was a substantial reduction (greater than 50%) in tillering associated with decreasing ϕ from $.81$ to $.33$, even though the amount of blue light in the same treatments increased from 50 to 117 $\mu\text{mol m}^{-2} \text{s}^{-1}$. The response to reduced phytochrome photoequilibria thus apparently overwhelms the response to blue light. This may be because the effect of blue light is saturating at fairly low fluence rates. Wheeler *et al.* (27) found the effect of blue light on the height of soybeans to be saturating at 30 $\mu\text{mol m}^{-2} \text{s}^{-1}$. At higher fluence rates of blue there may be no additional effect.

Dense canopies that selectively filter out more R than FR, creating low ϕ at the canopy bottom, act to reduce tillering and increase stem elongation. Reductions in ϕ , created by addition of FR at the base of plants in a sparse canopy, have the same effect. This suggests that radiation affecting these response is detected at least in part at the base of the plants (3, 8).

Thus, it may be that reductions in ϕ may only be necessary during early growth. After canopy closure, the canopy itself would create a low ϕ at the base of the plants, which would act to reduce tillering. Determination of the relative importance of the base of wheat plants as the site of perception would be of benefit to CELSS research. Further studies on the impact of within canopy enrichment to control tillering and the effect of phasic (different radiation regimes at different stage of plant growth) manipulation of radiation throughout the crop life cycle would also be useful.

Conclusions

1. Reductions in phytochrome photoequilibrium (ϕ) to levels simulating deep shade result in significant reductions in tillering of wheat.
2. Development of the main culm (Haun stage) is increased by increasing PPF and by reductions in ϕ .
3. Leaf sheath (but not leaf lamina) length are significantly increase by these reductions in ϕ .
3. Dry-mass accumulation is linearly related to PPF, but not significantly affected by reduced ϕ
4. No difference in tillering, dry-mass, or Haun stage resulted from using metal halide vs high-pressure sodium lamps.
5. The effect of blue light on morphological responses in wheat is small compared effect of reduced ϕ .

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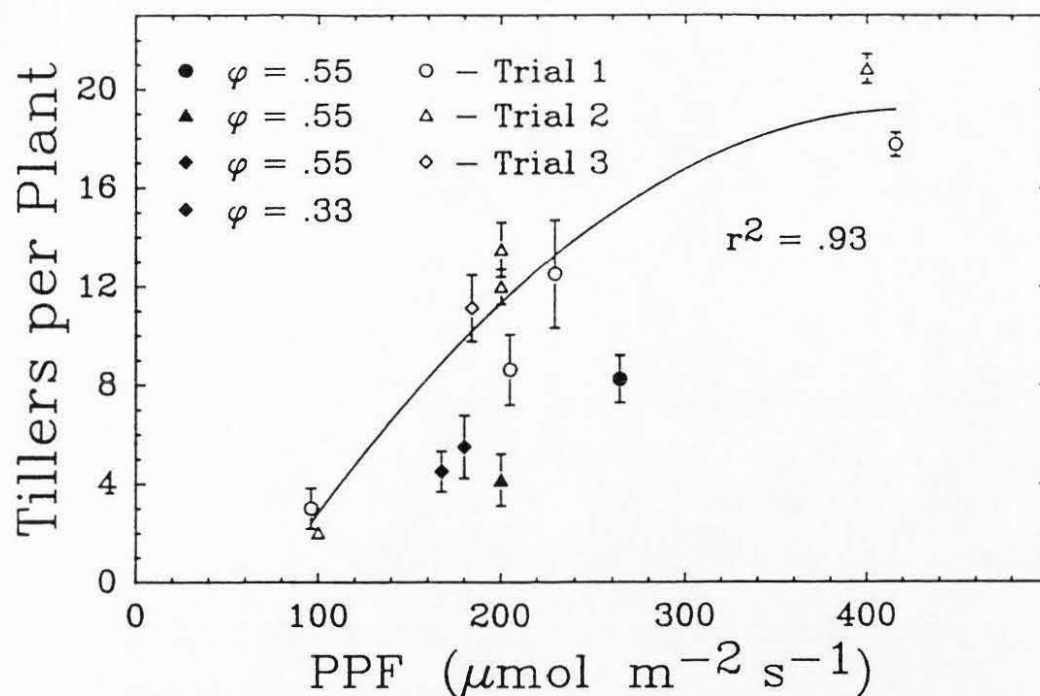


Fig. 1. Tillering response of cv Fielder to increasing radiation intensity (PPF). Solid symbols represent reduced phytochrome photoequilibria (ϕ) treatments and are not part of (2nd order) regression curves. Each data point is the average of 8 (trial 1) or 6 (trial 2 and 3) plants taken at the final harvest of each trial. Error bars are 95% CI.

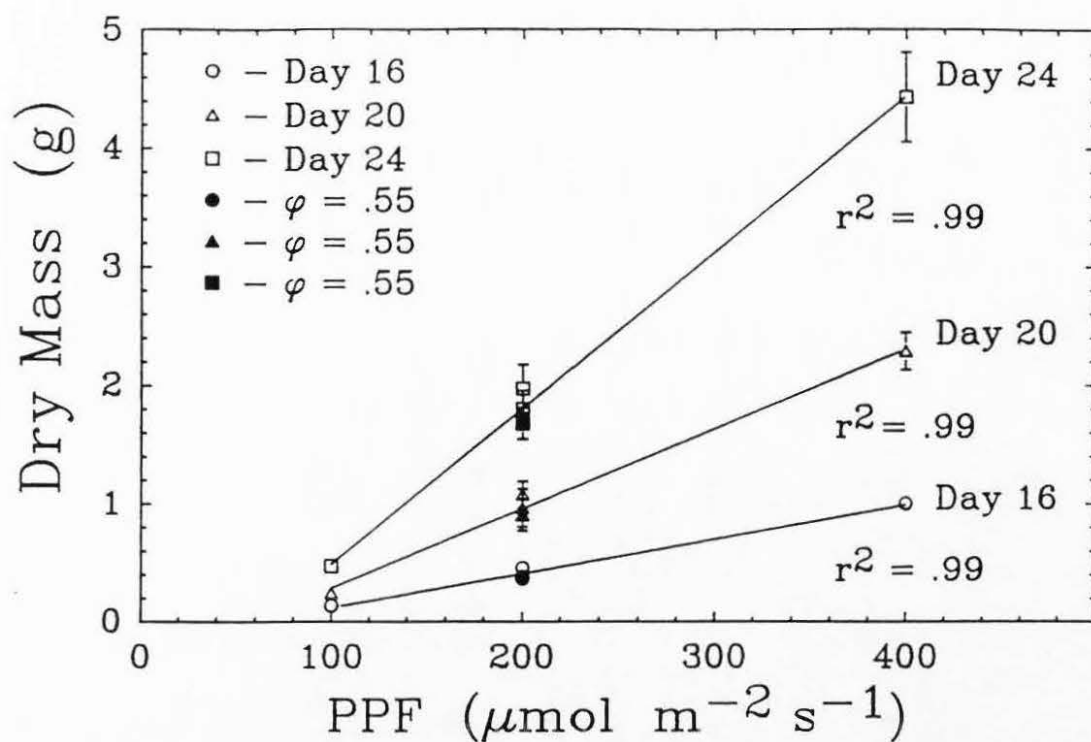


Fig. 2. Dry-mass accumulation (g) as a function of increasing PPF. Each data point represents the average of 8, 6, or 6 plants (cv Fielder) harvested 16, 20 and 24 days after emergence (trial 2). Error bars are 95% CI.

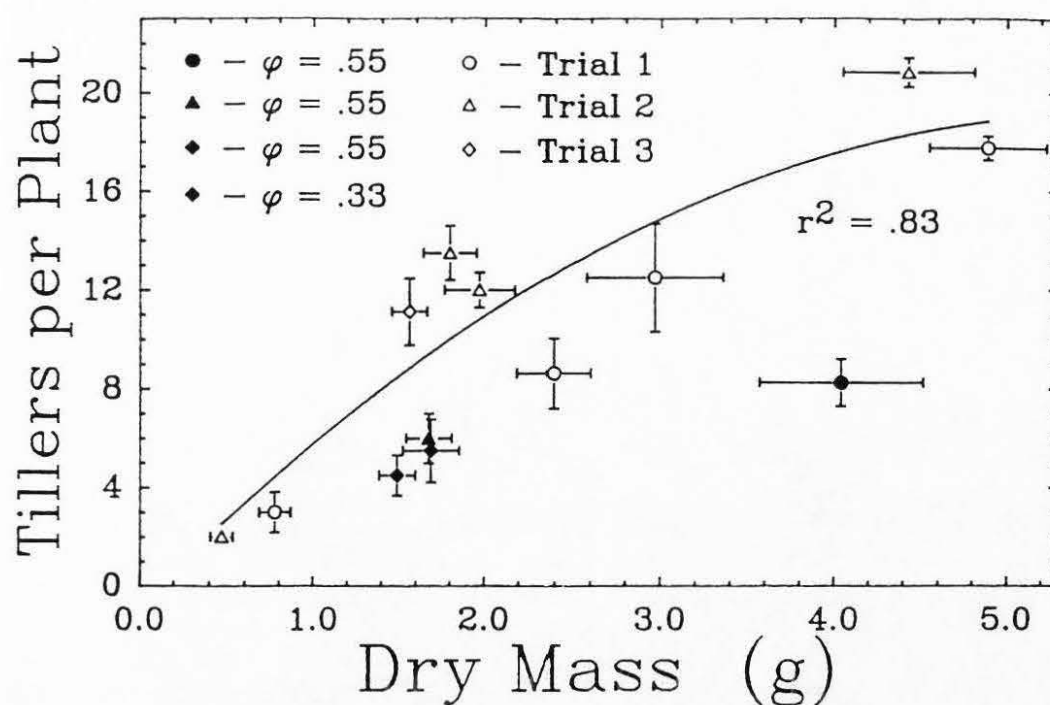


Fig. 3. Tiller production as a function of dry-mass. Data points are fitted to a 2nd order regression curve, except for the reduced ϕ values from each trial. Data points are averages of 8 (Trial 1) or 6 (Trials 2 and 3) plants (cv Fielder) taken at final harvest. Error bars are 95% CI.

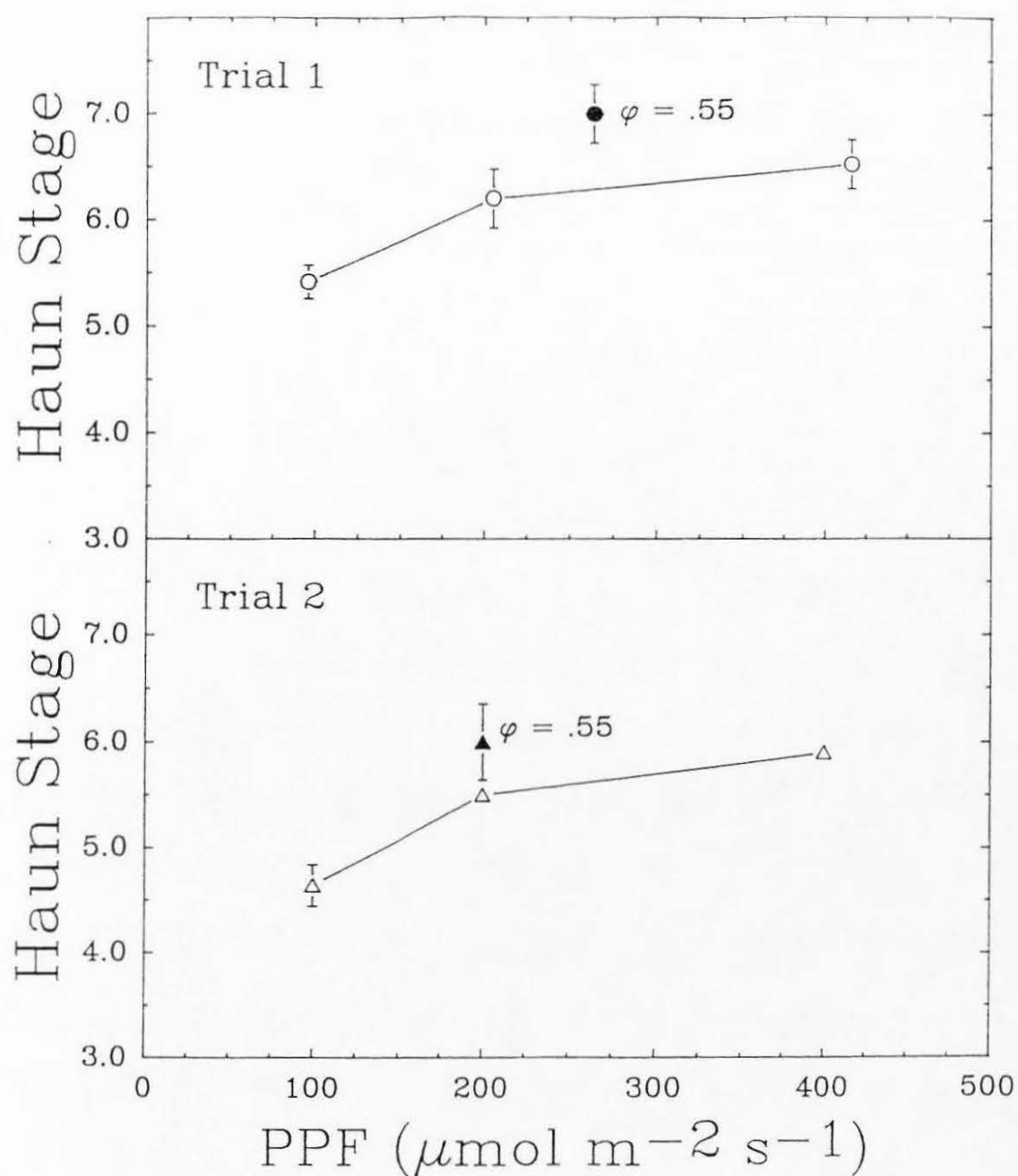


Fig. 4. Effect of reduced φ on main culm development (Haun stage). Data points are averages of 8 (trial 1) or 6 (trial 2) plants (cv Fielder) harvested 24 (trial 1) or 20 (trial 2) days after emergence. Error bars are 95% CI.

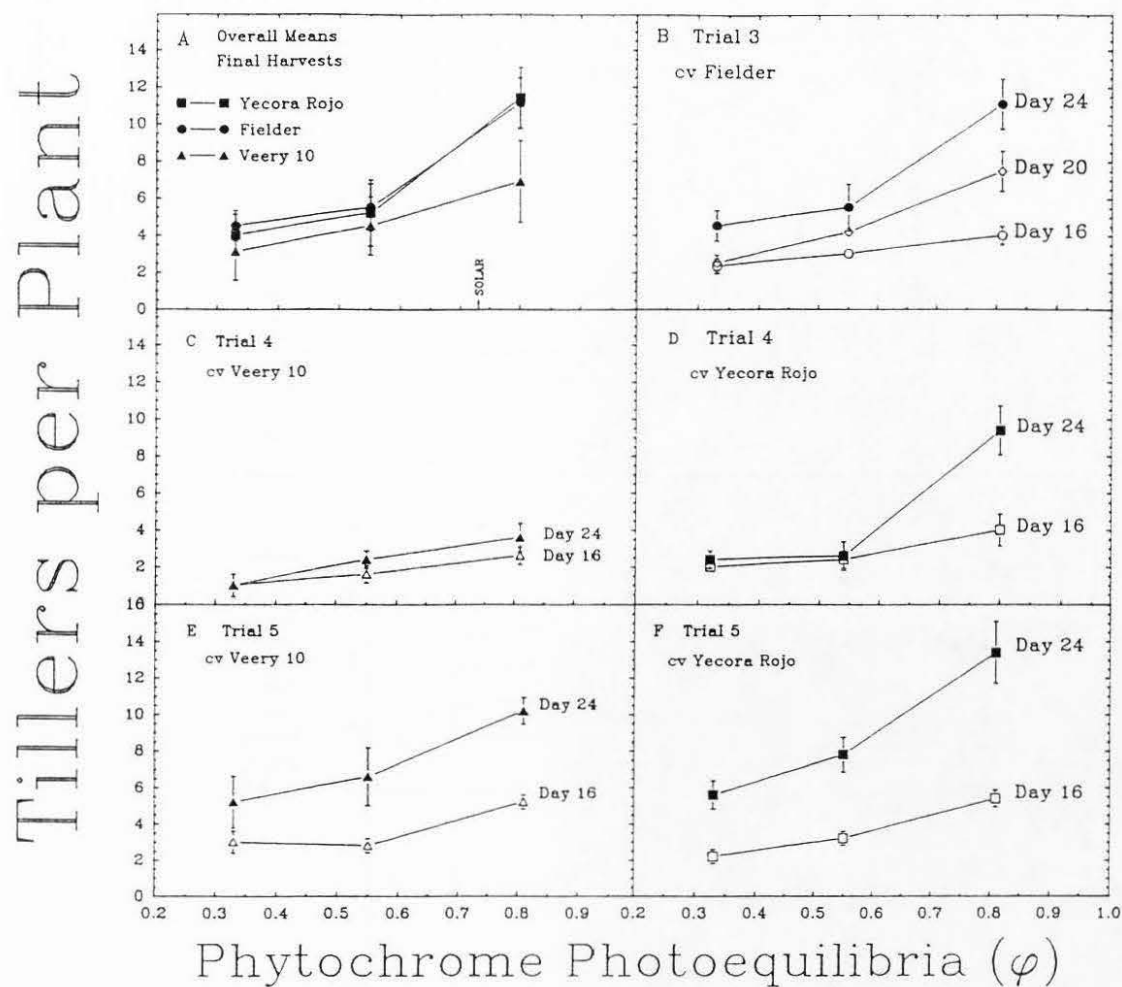


Fig. 5. Production of tillers in response to changing levels of predicted ϕ . Data points represent averages of 6 Fielder (trial 3) or 5 Veery 10 and Yecora Rojo (trials 4 and 5) plants from the final harvest of trials 3 - 5 (A); 8, 6, and 6 plants at each of three harvests for cv Fielder (B); and 5 plants at each of two harvests for both Veery 10 (C and E) and Yecora Rojo (D and F). Error bars represent the 95% confidence interval in all cases.

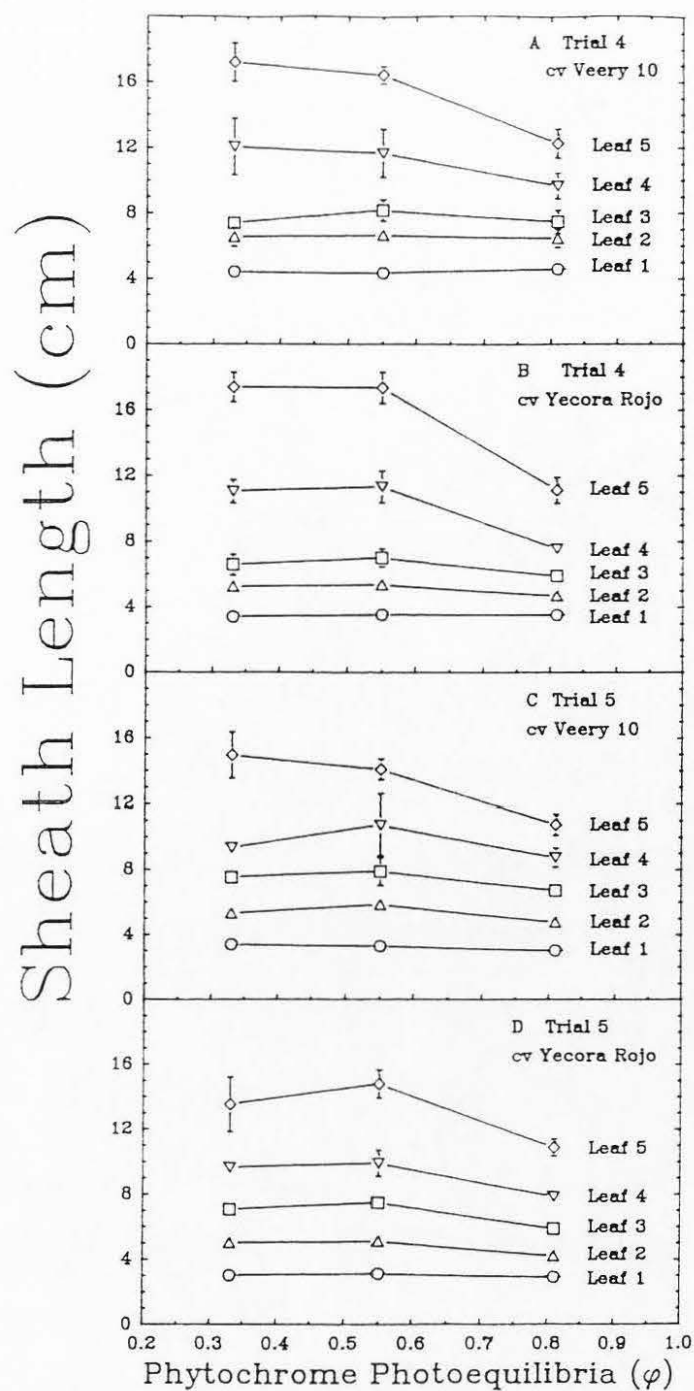


Fig. 6. Sheath and lamina length (cm) as a function of (ϕ). Each data point represents measurements of the first five emergent leaves of five cv Veery 10 and Yecora Rojo plants. Error bars are 95% CI.

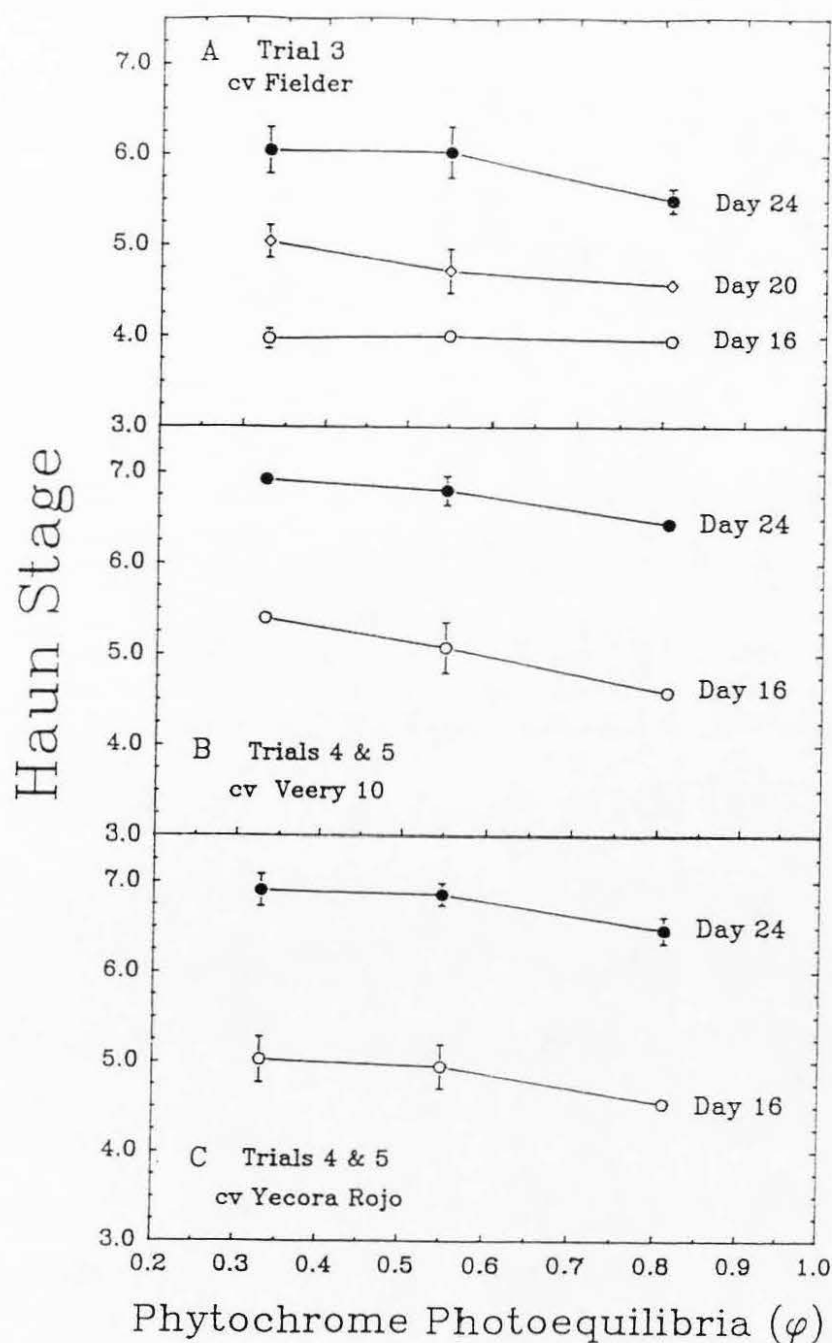


Fig. 7. Main culm development (Haun stage) as a function of ϕ . Values for each data point for cv Fielder represent 8, 6, and 6 plants for (Trial 3) harvests at 16, 20 and 24 days after emergence (A). Each data point for cvs Veery 10 (B) and Yecora Rojo (C) represents 10 plants: 5 from each of the final harvests (24 days after emergence) of trials 4 and 5 combined for each cultivar. Error bars represent 95% CI.

THE EFFECT OF DAYLENGTH AND END-OF-DAY FAR-RED RADIATION ON WHEAT GROWTH AND MORPHOLOGY

Abstract

Wheat (*Triticum aestivum* L., cultivars Yecora Rojo and Veery 10) plants were grown under 24 or 16-h photoperiods at the same daily photosynthetic photon flux (PPF). Some plants grown under the 16-h photoperiod were also exposed to 10 min end-of-day far-red irradiation. Tillering, measured as tillers per gram, was reduced for both cultivars by the addition of end-of-day far-red radiation but was not significantly affected by shortening the photoperiod from 24 to 16-h. Main culm development (measured as Haun stage) was reduced for both cultivars by the reduction in photoperiod from 24 to 16-h and by the addition of 10 min end-of-day far-red radiation. No change in leaf sheath or lamina length was observed for either cultivar in either the 24 versus 16-h comparison or the 16-h versus 16-h + end-of-day far-red comparison.

Introduction

Lower predicted phytochrome photoequilibria (ϕ)² have been shown to reduce tillering, increase leaf sheath length and increase main culm development (Haun stage) in wheat (*Triticum aestivum* L.) (1). Phytochrome activity and subsequent plant responses are also affected by dark periods and by end-of-day R and FR treatments. In the dark, P_{fr} , generally considered to be the active form of phytochrome, slowly breaks down (enzymatic degradation) or reverts to P_r , the inactive form (10) except in monocots, where dark reversion does not occur (4). The mechanism of action of phytochrome in photoperiodic effects, however, cannot be satisfactorily explained by this "hour-glass" analogy alone, and must be reconciled with the interaction of phytochrome activity and the biological clock (8).

Photoperiods act as "zeitgebers" (time givers) that entrain plants, resetting their endogenous rhythms to a 24-h "day" each time the plant experiences a dark period (8). The effect of this entrainment is to maximize the sensitivity of the plant to light signals at the end of the light period, especially sensitivity to FR (G. Deitzer, personal communication). Interaction of the endogenous rhythm with signals that alter ϕ (such as FR) accounts for the effect of end-of-day treatments on plant responses.

The effect of photoperiod on the rate of development in barley (*Hordeum vulgare* L.) and wheat was studied by Cao and Moss (2), who found that an

² Abbreviations: FR, far-red radiation (700-800 nm); R, red light (650-700 nm); ϕ , ratio of P_{fr} to P_{total} (total phytochrome)

increase in daylength from 16 to 24-h resulted in an increase in the rate of leaf emergence of 14% in barley and 9% in wheat.

Previous studies have demonstrated reduced tillering in *Lolium spp.* (3) and reduced tillering and increased leaf length in wheat (1) in response to end-of-day FR treatments. Casal (1) found that end-of-day FR increased sheath length in the 5th leaf of wheat (cv Buck Cimarron) in two trials. Casal (1) also reported an increase in lamina length for the same leaf, but only in one of two trials and only for one of four cultivars tested. It is not clear from his paper whether or not results for all the leaves measured for all cultivars tested support his reported data. Tucker (9) found a sharp reduction in side shoot production in tomatoes in response to increased FR.

A possible explanation of these results is that irradiating plants at the end of the light period with FR, when they are maximally sensitive to this stimulus, greatly reduces the amount of P_{fr} in the plants, resulting in inhibitory or promotive effects of P_{fr} similar to those of reduced phytochrome photoequilibria under continuous irradiation. The objective of this study was to determine the effect of photoperiod and end-of-day FR irradiation on wheat growth and morphology.

Materials and Methods

Cultural Procedures. Wheat (*Triticum aestivum* L., cvs Veery 10 and Yecora Rojo) seeds were sown into soilless media (equal parts peat moss, perlite and vermiculite) in plastic pots (120 X 120 X 100 mm) and germinated at 23°C in a multi-sectioned, controlled environment growth chamber. Each treatment section contained 20 pots. Ten plants were Veery 10 cultivar and 10 plants were Yecora Rojo. Plants emerged uniformly in each treatment after three days and were thinned to one plant per pot five days after planting. All plants were then of approximately equal size. Pots were rotated every 3-4 days to improve uniformity exposure to treatments.

All sections of the growth chamber were connected to a common air conditioning system, so CO₂ concentration, humidity and temperature were nearly identical. Temperature was maintained at $21.5 \pm .5^{\circ}\text{C}$ in all sections throughout each trial. The atmosphere was enriched with CO₂ to approximately 1000 $\mu\text{mol mol}^{-1}$ to maximize the rate of assimilation. The planting density, approximately 40 plants m^{-2} , was uniform in each section. Pots were watered daily with ca 300 mL of a complete nutrient solution.

Photoperiod Treatments. Three photoperiod period treatments (24-h, 16-h and 16-h + end-of-day FR) with identical total daily PPF ($17.3 \text{ mol m}^{-2} \text{ d}^{-1}$) were created. Plants in the 24-h treatment section were irradiated with a 400-W metal halide (MH) lamp (Sylvania) passing through a 5-cm water bath and 9-mm Plexiglass barrier (Dupont Lucite acrylic). Plants in the two 16-h photoperiod

treatments were exposed to radiation from 1000-W MH lamps (Sylvania) filtered as above. Radiation in all treatments created the same phytochrome photoequilibrium, $\phi = .81$ during the illumination period. In the 16-h + FR treatment, ten min of FR radiation at the end of a 16-h light period was supplied with a 500-W incandescent spotlight filtered through a sheet of Westlake Plastics (Lenni, PA) FRF 700 filter. The intensity of FR (700-800 nm) radiation was $3.3 \mu\text{mol m}^{-2} \text{s}^{-1}$.

Radiation Measurements. Phytochrome photoequilibria (ϕ) were determined with a computer-driven spectroradiometer (Hewlett Packard model HP-85 computer and an Optronics model 740 A spectroradiometer) using the method of Sager *et al.*, (7). Photosynthetic photon flux (PPF) in each treatment and the amount of FR radiation in the end-of-day treatment were determined from the same spectroradiometric data. PPF data were corroborated with a quantum sensor (Li-Cor model LI-188B).

Plant Measurements. Harvests of five plants each of Veery 10 and Yecora Rojo were made 16 and 24 days after emergence. At each harvest, tiller number, main culm development (Haun stage), and dry weight were determined. Haun stage is a measure of the development of cereal plants based on a comparison of the length of the latest leaf to emerge to the length of the previous leaf (5, 6). The lengths of the leaf sheath and lamina for each of the first five leaves were measured at each harvest.

Results and Discussion

Dry-mass accumulation was reduced by about 25% for plants of both cultivars grown in the 16-h light period treatment compared to the other two treatments (Fig. 1). The unexpected reduction in dry-mass in the 16-h photoperiod is not consistent with any of the previous studies of photoperiod effects and appears to be due to an unknown factor. Tillers per gram dry-mass may be a better indicator of tillering than tillers per plant. Indeed, tillers per unit dry-mass was constant over a 10-fold range of plant dry-mass (unpublished data). For this reason, environmental effects on tillering are best described on a per gram basis. Tillering on a per gram basis was to be affected by a reduction in photoperiod unless that reduction in photoperiod is accompanied by supplemental FR at the end of the light period (Fig. 2). These results for cv Yecora Rojo agree with the results of Deregibus *et al.* (3) and Casal (1) which show a reduction in tillering in response to end-of-day FR.

If the results are expressed on a tillers per plant basis, which does not take into account differences in dry-mass (Fig. 3), they become difficult to interpret.

A small decrease in main culm development (Haun stage) occurred in both the 16-h and 16-h + end-of-day FR treatments (compared to the 24-h treatment) for cv Yecora Rojo but not for cv Veery 10 (Fig. 4). This result for cv Yecora is not consistent with our previous findings on the effect of lowered ϕ but is consistent with the findings of Cao and Moss (2), who observed an increase in the rate of

leaf emergence with longer photoperiods. Main culm development may be more sensitive to photoperiod than to end-of-day FR in these treatments.

No difference was observed for either leaf sheaths or laminae of either cultivar in either 16-h photoperiod treatment compared to continuous irradiation (Fig. 5). The effect may be too small to measure. Further research needs to be conducted to determine if the lack of response, in some cases, to these treatments is real or if the effects are simply too small to detect under these conditions. Shorter photoperiods and a higher fluence rates of FR radiation may be necessary to fully elucidate a response.

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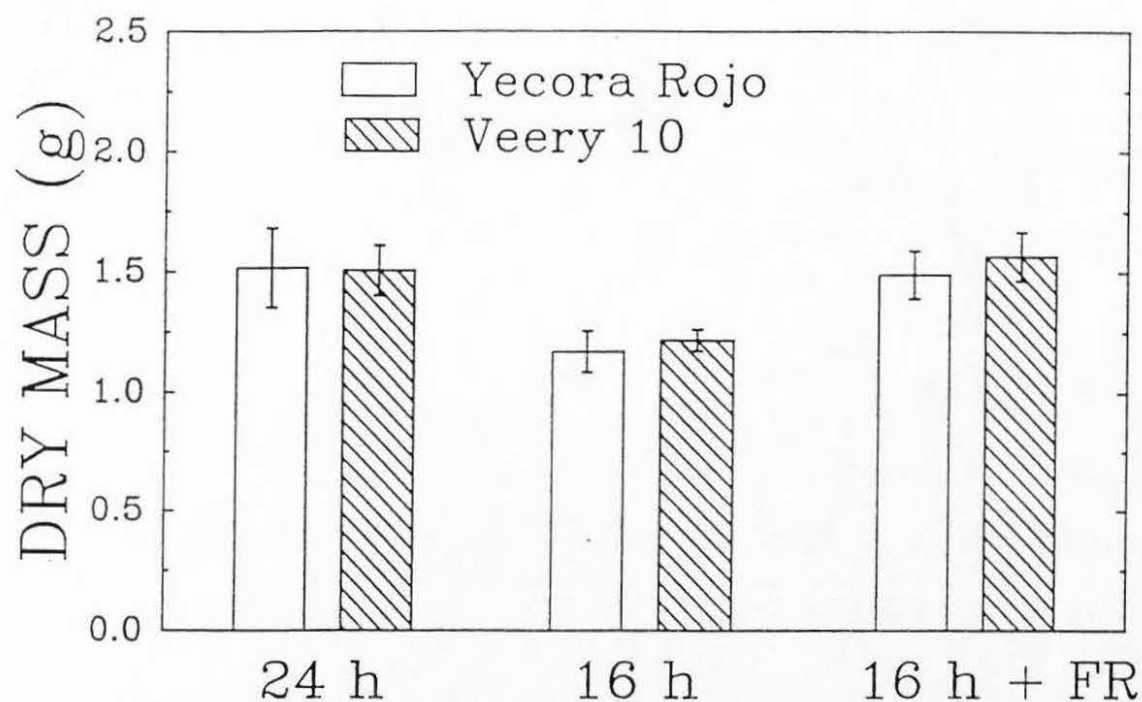


Fig. 1. Dry-mass accumulation (g) in response to daylength and end-of-day FR. Data are averages of five plants (cvs Yecora Rojo and Veery 10). Error bars represent 95% CI.

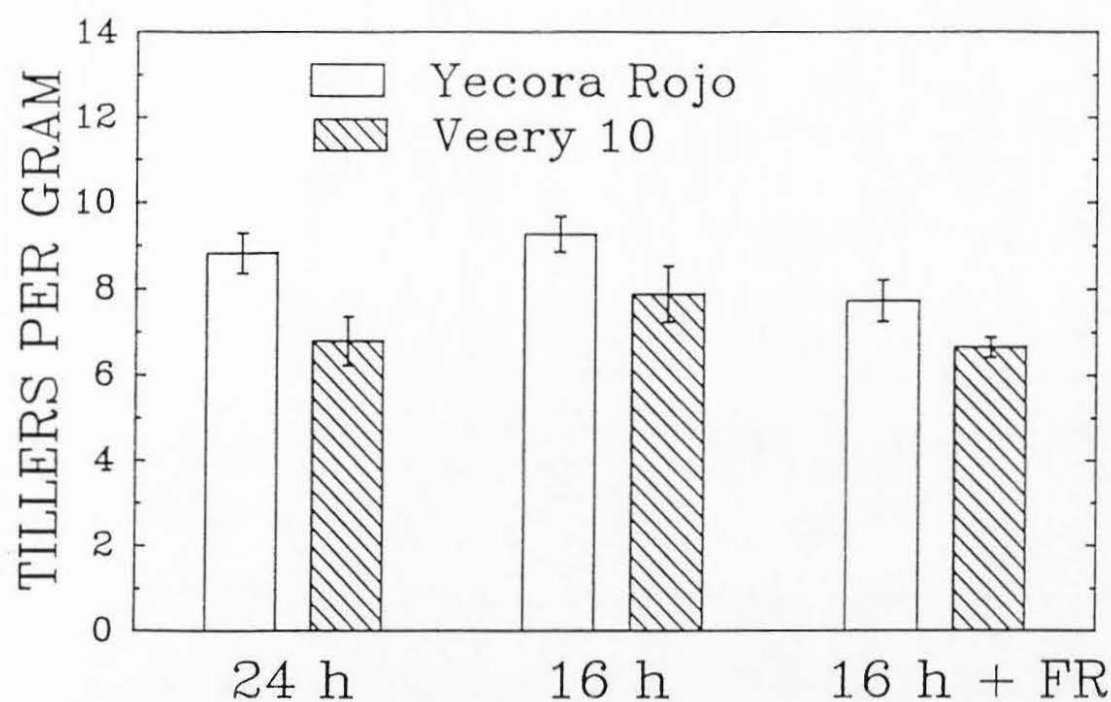


Fig. 2. Tillering response to daylength and end-of-day FR on a per-gram basis. Data are averages of five plants. Error bars represent 95% CI.

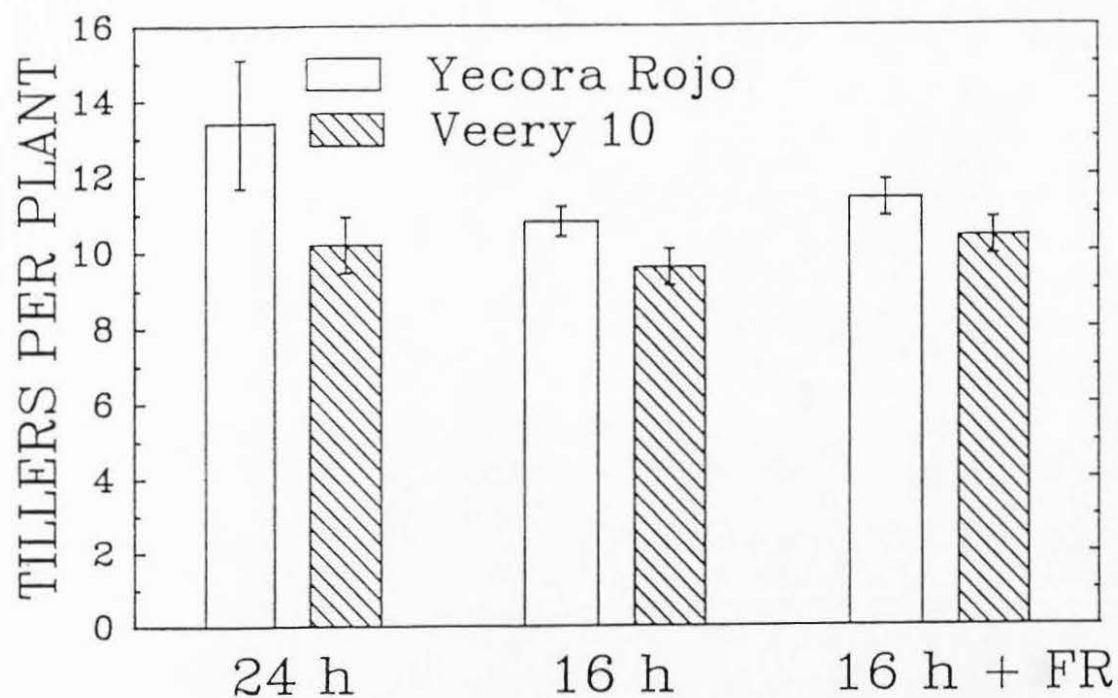


Fig. 3. Tillering response to daylength and end-of-day FR. Data are averages of five plants (cvs Yecora Rojo and Veery 10). Error bars represent 95% CI.

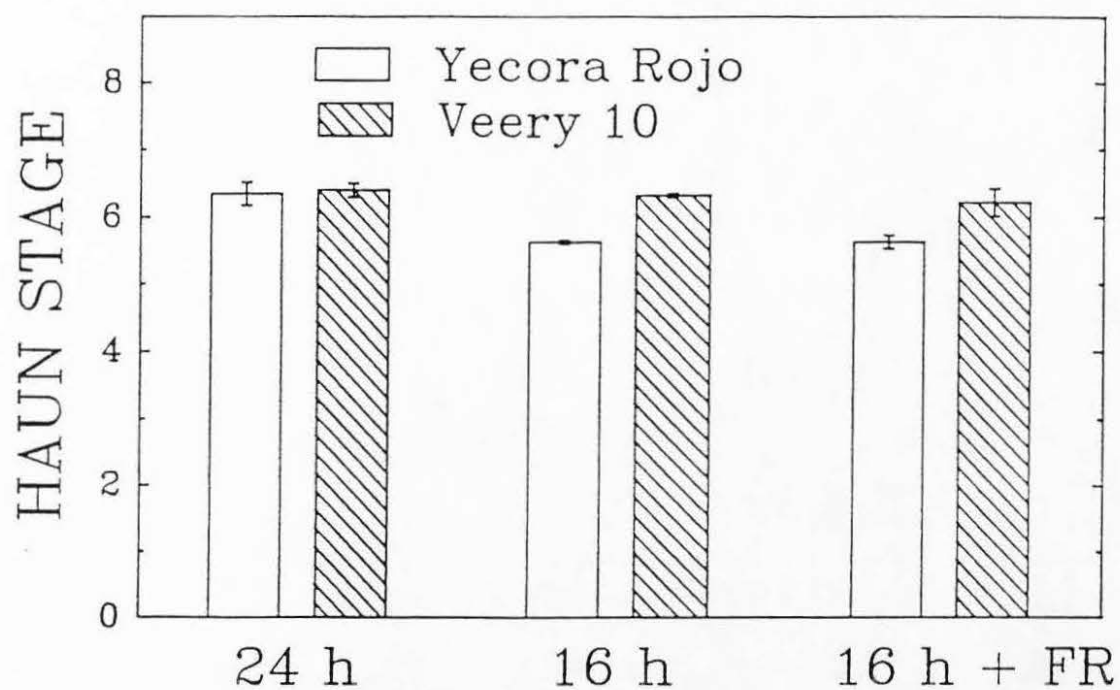


Fig. 4. Development of main culm (Haun stage). Data are averages of five plants (cvs Yecora Rojo and Veery 10). Error bars represent 95% CI.

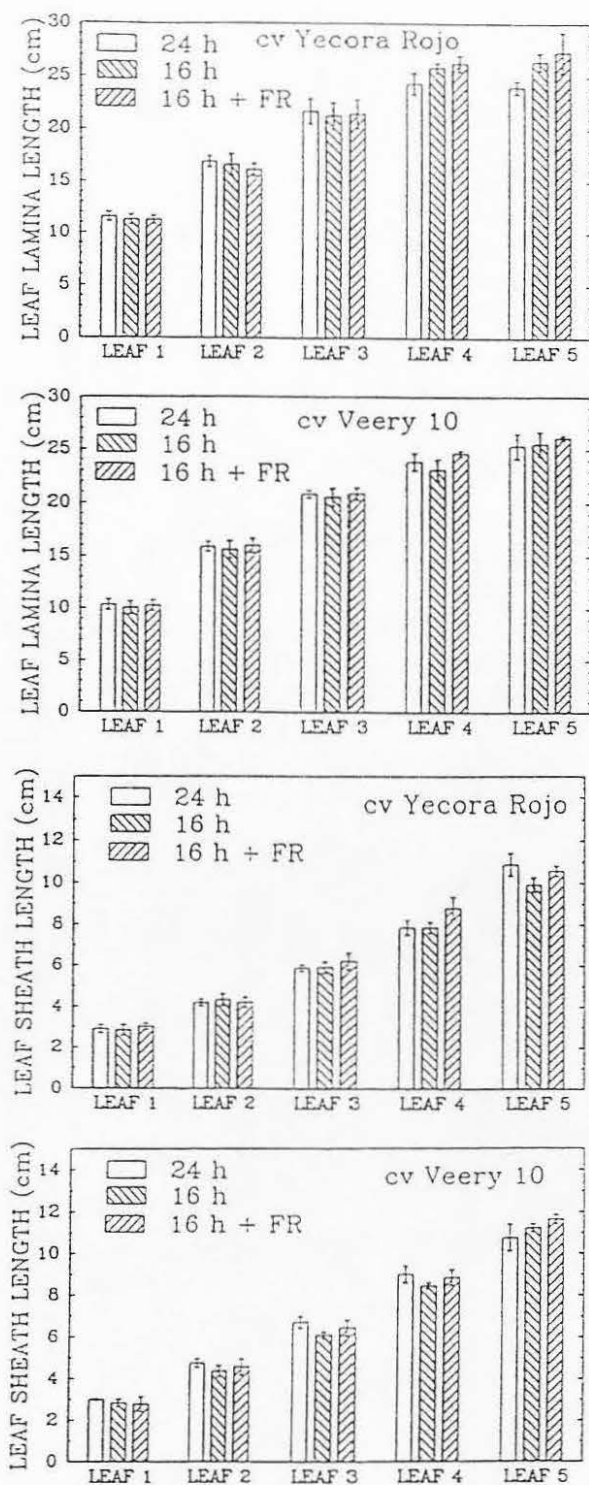


Fig. 5. Leaf sheath and lamina length (cm) response to daylength and FR. Data are averages for each of the first five emergent leaves of five plants each of cvs Yecora Rojo and Veery 10. Error bars represent 95% CI.

MORPHOLOGICAL RESPONSES OF WHEAT TO BLUE LIGHT

Abstract

Blue light significantly increased tillering in wheat (*Triticum aestivum*, L.) plants grown at the same photosynthetic photon flux (PPF). Plants were grown under two levels of blue light in a controlled environment with continuous irradiation. Control plants received $50 \mu\text{mol m}^{-2} \text{s}^{-1}$ of blue light, and treatment plants received $2 \mu\text{mol m}^{-2} \text{s}^{-1}$ blue light (400-500 nm wavelength) from filtered metal halide lamps. Both treatments received $200 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPF (400-700 nm). Tillering increased an average of 25% under blue light. Blue light also caused a small, but consistent, increase in main culm development, measured as Haun stage. Leaf length was reduced by higher levels of blue light. Plant dry-mass was not significantly affected by blue light. Applying the principle of equivalent light action, these effects are assumed to be mediated by the blue-UV light receptor(s) since phytochrome photoequilibria for each treatment were nearly identical.

Introduction

NASA's commitment to space exploration includes the development of a Controlled Environment Life Support System (CELSS) that will be an integral part of any off-world human colony (1, 9). Refinement of environmental conditions that optimize plant growth is an important facet of this effort (11). Studies of crops grown under low-stress conditions typical of those found in a CELSS indicate that wheat (*Triticum aestivum* L.) plants tiller more than plants grown in the field. Wheat crops that produce fewer tillers may be more productive in a controlled environment than those that tiller profusely for two reasons: 1) a crop composed of single-headed plants can be harvested earlier since the primary head of each plant matures first and, 2) primary heads have a higher harvest index (2). Thus, reducing or eliminating the tillering response of wheat plants in controlled environments would be beneficial to CELSS research.

The objective of this study was to determine the effect of blue light on morphological responses in wheat, especially tillering. Since plant height is also a concern in controlled environments (volume in a may be a limiting factor in a CELSS), and since blue light is known to inhibit stem elongation (5, 17), we also investigated this effect.

The exact mechanisms of blue light detection and subsequent plant response are not yet known. Rather than a single photo-sensing molecule, as in the case of phytochrome, the blue-UV light detecting mechanism in plants may be a group of photoreceptors. None of these hypothesized photoreceptors have been identified,

thus the nickname, cryptochrome (12). Cryptochrome may also act in concert with other photoreceptors, especially phytochrome, perhaps by enabling phytochrome to express its final action in many plant responses (8).

Absorption of blue light by higher plants results in a wide variety of responses. Cellular and sub-cellular responses include enzyme regulation, biosynthesis of anthocyanin and other pigments, enhancement of respiration, chloroplast rotation, and stomatal opening (13). At the organismal level, morphogenic responses such as phototropic curvature, flowering and growth inhibition and promotion have been traced to the action of the blue light receptor (13). Inhibition of stem extension in dicots by short term exposure (on the order of minutes or hours) to blue light (400-500 nm) has been demonstrated by many researchers (3, 5, 16, 17).

Few studies have been done on the long-term effect of blue light on mature plants. Wheeler *et al.* (18) reported blue-light-induced reductions in stem elongation for soybeans grown for 28 days under high-pressure sodium lamps. Increasing amounts of blue light at a constant PPF decreased stem elongation up to a maximum of 50% with $35 \mu\text{mol m}^{-2} \text{s}^{-1}$ of supplemental blue light, suggesting that suppression of stem extension by blue light in soybeans is saturated at this level.

Materials and Methods

Cultural Procedures. Wheat (*Triticum aestivum* L. cv Fielder) seeds were sown into soilless media (equal parts peat moss, perlite and vermiculite) in plastic pots (120 X 120 X 100 mm) and germinated at 23 °C in two sections of a six-sectioned, illuminated growth chamber (in which other experiments were simultaneously conducted). Each treatment section contained 24 (Trial 1) or 20 Trials 2-3) pots. Plants emerged uniformly in both treatments after three days and were thinned to 1 plant per pot 5 days after planting. All plants were then of approximately equal size. Pots were rotated every 3-4 days to improve uniformity. All sections were connected to a common air conditioning system so CO₂, humidity and temperature were nearly identical. Pots in both treatments were watered daily with approximately 300 mL of a complete nutrient solution. Temperature was maintained at $21.5 \pm .5$ °C in both sections throughout the trial. The atmosphere was enriched with CO₂ to approximately 1000 $\mu\text{mol mol}^{-1}$, to increase the rate of carbon assimilation.

Spectral Treatments. Control plants were exposed to white light ("high-blue" treatment) from a 1000-W metal halide (MH) lamp (Sylvania) passing through a 5-cm water bath and 9-mm plexiglass barrier (Dupont Lucite acrylic). Plants in the reduced ("low-blue") blue (400-500 nm) treatment were exposed to radiation additionally filtered through a yellow (Rosco R161 "Canary Yellow") filter that removed approximately 96% of the blue photons.

Radiation Measurements. Relative contribution of blue photons to total photosynthetically active radiation (PAR) in each treatment was determined with a computer-driven spectroradiometer (Hewlett Packard model HP-85 computer and an Optronics model 740 A spectroradiometer). Photosynthetic photon flux (PPF) was measured with the same spectroradiometer and corroborated with a quantum sensor (Li-Cor model LI-188B). Control plants ("high" blue treatment) received $200 \mu\text{mol m}^{-2} \text{s}^{-1}$ of continuous PPF, of which $50 \mu\text{mol m}^{-2} \text{s}^{-1}$ were blue photons. Plants in the low blue treatment also received a continuous $200 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPF, approximately $2 \mu\text{mol m}^{-2} \text{s}^{-1}$ of which were blue photons.

Phytochrome photoequilibria, the fraction of total phytochrome in the active state (Pfr/Ptotal, or ϕ), were determined ($\phi = .81$ for the high blue treatment, $\phi = .83$ for the low blue treatment) from the same spectroradiometric data using the method of Sager *et al.* (10).

Plant Measurements. At each harvest, tiller number, main culm development (measured as Haun stage, using the method of Klepper *et al.* [7]), dry weight, and the length of the longest fully extended leaf were determined. Detailed harvest procedures were as follows: **Trial 1.** Eight plants were harvested at 23, 25 and 28 days after emergence. **Trials 2 and 3.** Harvests were 8, 6, and 6 plants taken 16, 20 and 24 days after emergence.

Statistical analysis. All data was analyzed by ANOVA generating comparisons of the least significant difference (LSD) between means, based on student's t test.

Results and Discussion

One of the proposed mechanisms of the action of blue light is an enhancement or enabling of the action of phytochrome, so it is important that the potentially confounding effect of the simultaneous action of phytochrome be eliminated. This can be accomplished by employing the principle of equivalent action of light, which states that two treatments creating the same photostationary state for phytochrome (ϕ) will affect plant responses due to phytochrome identically (15). Differences in plant response under these conditions must then be ascribed to another photoreceptor or some other mechanism. Applying this principle to the blue light treatments in this study, the phytochrome photostationary states are nearly equal ($\phi = .81$ for the high blue treatment, $\phi = .83$ for the low blue treatment), so the blue-UV light receptor(s) becomes the probable causative agent for differences in plant response.

Effect of blue light on tillering. Wheat plants consistently produced more tillers when grown under normal MH lamp irradiation ("high blue" light: $50 \mu\text{mol m}^{-2} \text{s}^{-1}$) compared to plants grown under filtered MH lamps ("low blue" light: $2 \mu\text{mol m}^{-2} \text{s}^{-1}$). Plants produced an average of 25% more tillers under high blue light over three trials (Table I). Any possible effect of phytochrome on this response, due to the small difference in ϕ between the two treatments ($\phi = .81$ for "high blue" and $.83$ for "low blue"), can be disregarded because the slightly lower ϕ in the "high blue" treatment, if it had any effect at all, would result in fewer tillers, not more, as in this case.

Effect of blue light on dry-mass accumulation. No significant (based on LSD, student's *t*) effect of blue light on dry-mass accumulation was found (Table II). To eliminate the possibly confounding effect of plant size on tiller production, both tillers per plant and tillers per gram dry-mass were calculated (Table III). Plants grown under "high blue" light consistently produced more tillers/gram than plants grown under the "low" level of blue, verifying that the reduction in tillering was due to the effect of blue light.

Effect of blue light on leaf length. Leaves (measured as total leaf length) of wheat plants grown under low levels of blue light were longer (49.8 vs 45.2 cm, $P < .01$ - based on LSD, student's *t*) than those plants grown under high blue light.

Effect of blue light on main culm development. Main culm development (measured as Haun stage) was significantly enhanced by blue light for all three trials (Table IV). This result is somewhat surprising since it indicates that two different mechanisms of action may exist in wheat plants to mediate changes in main culm development in response to changes in blue light and phytochrome photo-equilibrium. Other research has shown that low levels of blue light have the same result as lower ϕ (Barnes, Morphological Responses of Wheat to Changes in Phytochrome Photoequilibria, in preparation). Tillering, for example, is reduced by both reduced ϕ and by low levels of blue light. Similarly, leaf length is increased by both reduced ϕ and by low levels of blue light. In these cases, the blue-UV light receptor(s) appears to be acting in concert with phytochrome in these responses.

The small difference in ϕ in the blue light treatments ($\phi = .81$ for "high blue" and $.83$ for "low blue") may be enough to account for the difference in Haun stage. Unlike tillering, the difference in ϕ is in the right direction to account for this change; previous research has shown that lower levels of ϕ result in increased development of the main culm. It is unlikely, however, that such a small difference in ϕ could cause the observed change in Haun stage (an increase of .3 Haun stage units with an decrease in ϕ from $.83$ to $.81$). In our previous work, reducing ϕ from $.81$ to $.33$ resulted in an increase of about .5 Haun stage units. Also, ϕ is near its maximum value (about $.89$) and responses to changes in ϕ in that region of values are negligible (14).

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Table I. *Effect of Blue Light on Tiller Production*

Data are means of tillers produced per plant, from the final harvest in each trial. Letters indicate significance at $P < 0.001$ level.

Treatment	Trial 1	Trial 2	Trial 3	Mean
High Blue	12.50	13.50	11.13	12.38 a
Low Blue	10.50	9.00	10.25	9.92 b

Table II. *Effect of Blue Light on Dry Mass Accumulation*

Data are means (g) from the final harvest in each trial. Letters indicate significance at the $P < 0.1$ level.

Treatment	Trial 1	Trial 2	Trial 3	Mean
High Blue	2.97	1.80	1.56	2.11 a
Low Blue	2.88	1.56	1.61	2.02 a

Table III. *Tillers Produced per Gram Dry Mass*

Values are from the final harvest of each trial. Letters indicate significance at the $P < 0.01$ level.

Treatment	Trial 1	Trial 2	Trial 3	Mean
High Blue	4.29	7.60	7.10	6.33 a
Low Blue	3.81	5.83	6.30	5.31 b

Table IV. *Effect of Blue Light on Haun Stage.*

The effect of blue light on main culm development, measured as Haun stage. Data are from the final harvest in each trial.

Letters indicate significance at the $P < 0.001$ level.

Treatment	Trial 1	Trial 2	Trial 3	Mean
High Blue	6.24	5.67	5.50	5.80 a
Low Blue	6.03	5.42	5.06	5.50 b

CONCLUSIONS

Manipulation of the spectral environment was shown to be effective in reducing the tillering response in wheat (*Triticum aestivum* L.). Radiation treatments that 1) created lower predicted phytochrome balance in the plants, 2) reduced the amount of blue light (400-500 nm), or 3) irradiated plants with supplemental end-of-day FR radiation, all acted to reduce the number of tillers produced. Lowering the phytochrome photoequilibria (ϕ) from 0.81 to 0.33 was the most effective treatment for reducing tillering, yielding reductions greater than 50%. Reducing the amount of blue light from 50 to 2 $\mu\text{mol m}^{-2} \text{s}^{-1}$ reduced tillering by 25%. Supplemental end-of-day FR reduced tillering (on a per gram basis) by about 10%.

In addition to reducing tillering, these spectral treatments also affected several other morphological responses in wheat. Lowered ϕ acted to increase the rate of development of the main culm (measured as Haun stage) and to cause greater elongation of wheat leaf sheaths. Reduced blue light decreased Haun stage and increased the elongation of both leaf sheaths and laminae. End-of-day irradiation with FR acted to reduce Haun stage slightly but had no effect on leaf length. None of the treatments affected dry-mass accumulation.

In general, wheat plants were more responsive to changes in phytochrome photoequilibria (ϕ) than to blue light. Large changes in ϕ and blue light in the

same treatment always resulted in changes consistent with predictions based on ϕ but which were opposite to those expected due to the effect of blue light.

Although these results are promising for improving crop yield in controlled environments, such as those used in NASA's Controlled Environment Life Support System (CELSS) project, further research is needed to determine the radiation requirements at all stages of the plant's life cycle for crops growing under the high light and high density conditions typically found in a CELSS. What is appropriate for young plants in a sparse canopy is unlikely to be optimal for mature plants in a densely planted CELSS.

APPENDIX

Phytochrome and Photoequilibrium. The effect of changes in the ζ ratio on phytochrome photoequilibria (ϕ) in plants has been measured directly (in vitro) in young tissue using a dual beam spectrophotometer (Gardner and Graceffo, 1982; Smith and Holmes, 1977 III). Unfortunately, phytochrome cannot be readily measured in mature green tissue due to the interference of chlorophyll. Because direct measurement of phytochrome in green tissue is difficult, researchers have developed methods to predict ϕ from measurements of the spectral energy distribution (SED) in the radiant environment.

Smith and Holmes (1977 III) correlated the phytochrome photoequilibrium (symbol: $\phi = P_{fr}/P_{total}$) in etiolated tissue grown under natural and artificial radiation systems with ζ , which allowed them to use ζ to predict ϕ . The value of ϕ varied from <0.2 within a wheat canopy to 0.54 above the canopy in natural daylight and was closely correlated with ζ over the range of 400-800 nm. When ζ was between 0 and 1, small changes in ζ resulted in very large changes in ϕ . Thus, reducing ζ to very low levels would apparently produce very low levels P_{fr} , thereby reducing tillering. The ζ ratios of 5.0 and 1.5 used by Kasperbauer and Karlen (1986) would result in ϕ that differed by only a small fraction.

Gardner and Graceffo (1982) developed a more accurate method of predicting phytochrome photoequilibria (ϕ), which takes into account a broader range of radiation. This method may be particularly important in environments with artificial radiation, where the SED is not identical to sunlight and predictions of ϕ from ζ based on sunlight SED are not valid (Figure 3a). Most artificial radiation

sources such as cool white fluorescent lights have a stronger blue component than natural sunlight. This blue radiation, as well as radiation of many other wavelengths, affects the balance of phytochrome and so needs to be included in the calculation of phytochrome photoequilibrium (ϕ). In their calculation of ϕ , Gardner and Graceffo use the quantum yields (ϕ') for photoconversion of P_r to P_{fr} and P_{fr} to P_r , which have been previously determined by other researchers for each 2 nm interval from 360 to 800 nm. The validity of these ϕ' values is based on the assumption that monochromatic red radiation (660 nm) creates a photoequilibrium at which P_{fr} comprises 75 or 80% of total phytochrome (P_t). Mancinelli (1986) reported that other, more recent studies estimated this equilibrium (P_{fr}/P_t at 660 nm) as high as 89% P_{fr} . In addition, Mancinelli lists recent values for P_{fr}/P_t for wavelengths from 670 to 730 (by 10 nm intervals) that differ from those given by Gardner and Graceffo. These values (ϕ') are multiplied by the photon fluence rate (I) measured for each interval and then summed over the entire range. The sum of the conversion of P_r to P_{fr} divided by the total of the sums of both conversions gives:

$$\phi = \frac{\sum (\phi'_{r,\lambda} * I_{\lambda})}{\sum (\phi'_{r,\lambda} * I_{\lambda}) + \sum (\phi'_{fr,\lambda} * I_{\lambda})}$$

$\phi'_{r,\lambda}$ = relative quantum efficiency of converting P_r - P_{fr} at λ .

$\phi'_{fr,\lambda}$ = relative quantum efficiency of converting P_{fr} - P_r at λ .

I_{λ} = photon fluence rate at λ , for $\lambda = 360$ to 800 nm, by 2 nm.

Predicting Phytochrome Photoequilibrium. The spectra of the radiation sources tested ranged from 300 to 800 nm. Spectra were analyzed with an Optronics spectroradiometer, operated by a Hewlett Packard 85 computer. This was used to predict the phytochrome photoequilibria (ϕ) above and within a wheat canopy according to the method of Gardner and Graceffo (1982). An HP-BASIC program was written for the over 600 separate calculations from each spectral measurement needed to calculate ϕ . The spectroradiometer and a LiCor quantum sensor were used to evaluate the reduction of photosynthetically active radiation (PAR) by various filters.

Creating Altered Red:Far-red Environments. Three methods can be used to reduce the red:far-red radiation ratio (ζ) and, therefore, (ϕ):

- 1) far-red radiation can be increased with supplemental sources,
- 2) red radiation can be reduced with filters, or
- 3) both methods can be employed simultaneously.

Red radiation can be filtered out with blue-green filters and the total PAR reaching the plant may remain high enough for acceptable growth. Candidate filters can be analyzed with the spectroradiometer to measure the SED and a LiCor quantum sensor to determine the reduction in PAR. Far-red enrichment seems a more promising method because it does not reduce total PAR reaching the plant. Both far-red enrichment and red radiation reduction by filtration may be necessary, however, for very low ζ ratios under artificial lamps that are strong red radiation emitters. We currently use high pressure sodium (HPS) and/or cool

white fluorescent lamps, both with ζ ratios about 30% higher than sunlight (Gardner and Graceffo, 1983). PPF levels of these radiation sources range from 1000-2000 $\mu\text{mol m}^{-2}\text{s}^{-1}$, which our high yields require. Reducing the PPF input with filters that block red radiation would reduce growth and yield. Alternatively, supplemental far-red radiation sources would not reduce the amount of PAR reaching the plant. Radiation from an incandescent bulb filtered through a Westlake Plastics FRF 700 filter, which is designed to block out nearly 100% of all radiation below 700 nm, is be an excellent source of supplemental far-red radiation. HPS lamps produce a ζ ratio of about 2 with an output in the range of about 20 and 10 $\text{mW m}^{-2}\text{nm}^{-1}$ at 660 and 730 nm, respectively; therefore, supplemental far-red radiation equivalent to only a few percent of the total output of 1000 Watt incandescent bulb could alter the ζ ratio (and therefore ϕ) sufficiently to test the general hypothesis.

End-Of-Day Irradiation. The effectiveness of continuous far-red enrichment vs end-of-day treatments were studied by growing plants under MH lamps with brief exposure to far-red radiation at the end of their photoperiods. The same photoperiods and irradiation levels were used for controls, but plants will receive no supplemental far-red radiation. The end-of-day exposure need not be more than a few minutes as the phototransformations of P_r to P_{fr} and P_{fr} to P_r occur rapidly, the majority of the change taking place in the first 10 s (Figure 4 a & b, from Smith and Holmes 1977, III). Mancinelli (1986), has found that 98 - 99% of the photoequilibrium value is achieved in 10 minutes.

Duration of Treatment. In dense wheat canopies, the value of ζ drops rapidly with depth to a minimum (the lowest value reported is 0.05). Other studies suggest that plants detect alterations in the red:far-red ratio at their base. We recently found that PPF absorption approaches 98%, 15 to 18 days after germination in developing wheat canopies of densities 3500 and 7000 plants/m². The approximate maximum absorption is 98%, since about 2% is reflected by the canopy. At high densities, absorption exceeds 90% after day 10.

PAR absorbance is highly correlated with a reduction in the red:far-red radiation ratio (ζ) and phytochrome photoequilibrium (ϕ). A wheat canopy that attenuates 90% of incident PAR has an LAI of approximately 3-4 (unpublished data). Smith and Holmes (1977) found ζ values were around 0.2 when the LAI was 3 or higher. A 10-day old, high-density wheat canopy with an LAI of 3 might thus be expected to absorb 90% of the incident PAR and reduce ζ to a value of 0.2 and ϕ to a value somewhat below 0.2. Research efforts, therefore, should be focused on the first 10-20 days of growth, when wheat canopies are more open and treatment irradiation is incident on the entire plant. Once the canopy fills in, ϕ should drop to a low level at the stem base, regardless of the red:far-red radiation ratio in the incident radiation above the canopy. Altering the ζ ratios above a closed, dense wheat canopy may not affect % P_{fr} and tillering.

Determination of Tiller number. Tillers are formed in the axil of each leaf on the main stem and in the axils of leaves on each tiller (Klepper et al. 1982). They may also appear at the coleoptilar node, which is the second node produced but is

generally the lowest node to produce tillers (Esau, 1977; Klepper, et al. 1982).

Williams et al. (1975) have shown that microscopic examination of transverse and longitudinal sections of the stem base can reveal the number and location of tiller buds and tiller bud primordia. The method of Klepper et al. (1982) for assigning exact numerical values for tillering and culm development (Haun stage) can be used to identify both emerged tillers and pre-emergent tiller buds.

Site of Perception. Where do plants detect SED changes? It has been suggested they detect ζ ratios at their base because dense canopies tiller less than sparsely planted ones. Phytochrome, however, is well distributed throughout the plant and dense canopies contain much phytochrome that is exposed to higher ζ ratios. It may be the total plant phytochrome balance that controls the tillering response rather than the local ϕ at the base. Studies by Smith and Holmes indicate above-canopy radiation creates a gradient of ϕ values from the top of the canopy to the bottom. Side irradiation with supplemental red radiation would create a lateral gradient through the canopy in which all plants receive more evenly distributed red from top to bottom, although leaves will filter the red radiation more than the stem bases. Comparison of tillering and calculated ϕ for these two treatments (above-canopy and side irradiation) may help localize the site of perception. At some point in each ϕ gradient, tillering will be equal.

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